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Studies in Cell-division.

BY DOUGLAS H. CAMPBELL.

(Plates CII. and CIII.)

The following paper was written, not so much as a contribution to our knowledge of the subject, as to call the attention of teachers of botany to several characteristic and accessible examples for demonstrating easily the most essential points in this very important subject.

It is a common idea that the study of cell-division, especially the division of the nucleus, is a very difficult subject for anyone not thoroughly versed in histological methods, and while this is in many cases true, nevertheless it is possible to find cases where these processes can be readily studied with very little aid from reagents, and indeed in some instances followed through in the living cell.

The last ten or fifteen years have seen a great advance in our knowledge of these processes. Up to about 1875, in which year the first edition of Strasburger's "Zellbildung und Zelltheilung" appeared, the general belief current was that of Hofmeister, who believed that in all cases of cell-division the nucleus first became dissolved and that subsequently new nuclei were formed from the cell-plasma previous to the division of the latter. Since the appearance of Strasburger's book the subject has attracted the attention of many of the ablest zoologists as well as botanists, among whom none have done more than Strasburger himself.

The results of these investigations show that every nucleus (with a few doubtful exceptions) arises from the division of a pre-existing one, and that among plants, at least, the origin of a nucleus from undifferentiated protoplasm never occurs.

In the simplest plants, like the Schizophytes, it is probable that in most cases the nucleus substance is not concentrated in the form of a definite nucleus, though such a body has been demonstrated in a number of the larger *Cyanophyceæ.* The latest investigations of Zacharias in this subject leave the question of the presence of nuclei in these forms still open. In these plants, especially those that are truly unicellular, or with cells only slightly coherent, we find the simplest form of fission, a mere constriction of the cell, without any participation of the nuclear substance beyond the mere mechanical separation of the portions in the two daughter cells.

In *Nostoc*, (Pl. CII. Fig. 1) we can usually find filaments in which all stages of cell-division are present, and the process is easily followed. The resting cells, (1), are nearly globular. Previous to division they elongate in the direction of the axis of the filament, (2), and a slight constriction appears in the middle of the cell, (3). Later stages (4-6) show this constriction deeper, until finally the daughter cells are completely separated by the formation of a division wall, and becoming rounded off, assume the form of resting cells.

The first plant in which the process of cell-division was carefully studied, and one of the best for showing simple fission, is *Cladophora.* The common species are found in almost every stream, and may be kept indefinitely in the laboratory.

The cells are multi-nucleate, which may be shown by fixing the cells with one per cent. chromic acid in water, thoroughly washing and staining with borax-carmine or alum-cochineal. The nuclear division is not easily shown, and takes place independently of the cell-division.

The latter may almost always be found by examining a lot of actively-growing filaments, and when once found may be followed through in the living cell. The later stages may be quickly recognized, even when but slightly magnified, the green contents of the cell being pushed away from the outer wall of the cell by the advancing division-wall. If such filaments are now more strongly magnified and the other cells carefully examined, we shall probably find some in which the process is just beginning. In these (Pl. CII. Fig. 2) the young division-wall appears as a fine ring running around the middle of the cell, its edge directed toward the center of the cell-cavity, and pushing in the protoplasmic sac, leaving an evident clear space between the latter and the side walls of the cell. In larger cells, especially, (Fig. 7) it is very evident that the chloroplasts and other granular contents of the cell, do not occupy the extreme periphery of the protoplasmic sac, but that this is composed of perfectly homogeneous colorless plasma (Ectoplasm).

If we wish to follow the process through in the same cell, it is better to choose a rather small one, as the division does not take so long as in the larger ones. At ordinary temperature (20°-25° C.) the whole process in such cells takes from four to five hours.

The division of the inner granular protoplasm is completed some time before the division wall is closed, so that there is a neck of perfectly colorless protoplasm connecting the two green masses for some time before the connection between the daughter cells is completely severed, (Figs. 4, 5), and for some time after the division is completed the chloroplasts and other granules are contracted away from the division wall (Fig. 6).

Similar to the process just described is what occurs in the different species of *Spirogyra* and similar forms. The great difference lies in the fact that cell-division is accompanied by the division of the single nucleus of the cell.

Cell-division in the various species of *Spirogyra* takes place normally at night, but it may be retarded by suddenly reducing the temperature shortly before the time at which division would ordinarily begin, and keeping the plants in this condition until wanted. In cool weather, when the temperature sinks to near the freezing point at night, it is generally sufficient to keep the plants in a warm room during the day, and at about 10 p. m. to place the vessel containing them out of doors for the night. If they freeze slightly it will ordinarily do little harm. On bringing the plants into the laboratory in the morning, some of the cells will be pretty certain to begin division almost immediately.

The details* of the nuclear changes are not very easy to follow, but such stages as shown in Pl. CII. Fig. 8 are often met with. We find in such the division wall forming in the same way as in *Cladophora*, but near the center of the cell-lumen we find two daughter-nuclei suspended by protoplasmic threads and joined by numerous fine filaments, the outer ones of which are attached to the margins of the advancing division wall. The protoplasmic body of the cell is cut through in precisely the same way as in *Cladophora*, and finally the daughter nuclei move to the centers of the new cells.

The various desmids, especially the forms with constricted cells, show an interesting modification of the process observed in *Spirogyra*. Desmids are especially common on such fine-leaved aquatics as *Naias*, *Nitella*, *Chara*, and especially *Utricularia*, whose finely dissected leaves are often in late summer and autumn loaded down with all sorts of micro-organisms, among which are many of the most beautiful desmids. With a little care these may be kept in glass jars or other convenient vessels and will thrive for a long time. In such cultures they are not infrequently met with undergoing division, which occurs at all hours of the day.

The first sign of approaching division is the elongation of the neck connecting the semi-cells. A circular split in the wall is formed at this point and widens rapidly, forcing the original semi-cells apart, when these appear connected by a slender, colorless cylinder with much thinner walls than the original semi-cell. As this connecting cylinder enlarges it soon becomes constricted in the middle, and a division wall is formed much as in *Spirogyra*, this being accompanied by the division of the centrally placed nucleus. As division proceeds the two halves of the colorless neck enlarge rapidly, forming colorless vesicles lying between the original semi-cells which as yet contain all the colored contents of the cells. (Such a stage is shown in Pl. CII. Fig. 9). Here we find that the single large chloroplast in each half of the original cell is becoming constricted as well as the pyrenoid (p.) imbedded in it, and that the nuclear division is completed. In a somewhat later stage the lower halves of each chloroplast push down into them, and finally separate completely from the part that remains in the old semi-cell.

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*Strasburger—Das Botanische Practicum—p. 612 1st. Edit.

The whole process under proper conditions, is completed in about two hours, but care must be taken that the temperature of the water in which the specimen is mounted is about the same as that from which it is taken. A marked rise of temperature is apt to kill the cells.

For studying the complicated changes that the nucleus undergoes during cell-division, as well as the method of the formation of the division-wall as it usually occurs, we must examine some of the higher plants.

For following the process in the living cell, probably no plant is better than *Tradescantia Virginica.*

Strasburger showed* that the stamen hairs of this plant were especially useful for this purpose, and has described the process so fully in several places that it will not be repeated here. For examination it is only necessary to carefully remove the stamens from young buds and mount them with the attached hairs in water or a weak (three per cent.) solution of sugar in water. It is possible to stain these† without killing them, by using a weak aqueous solution of methyl-violet, dahlia or mauvein but very little more can be seen than in the unstained cells and the process of division is retarded.

For easy demonstration of the process of karyokinesis, the final divisions of the pollen mother-cells, especially of monocotyledons, are the best subjects.

Among dicotyledons which, as a rule, are unfavorable for showing the finer details of the nuclear divisions, *Podophyllum peltatum* is a conspicuous exception, and the process will be described somewhat in detail for this plant, with some reference also to a common and easily studied monocotyledon, *Allium Canadense.* In *Podophyllum* buds should be taken just as the plants appear above ground in the spring. The same young umbel of *Allium* often furnishes different stages, and with a little care all stages may be found, and very satisfactorily shown by the following simple method : The young anthers are removed and carefully crushed in a drop of equal parts ordinary acetic acid and distilled water, placed on a clean slide. The pollen mother-cells will be thus set free in the fluid, which fixes them instantly. The preparation may now be examined with a low power to see if the desired stages are present. If this is the case a drop of staining fluid should be added and a cover-glass placed over the preparation. I have obtained most beautiful results by using gentian-violet. A little of a strong alcoholic solution of this stain is diluted with several volumes of weak acetic acid, (about one part acid to two of water), and a drop of the stain thus diluted is added to the preparation. As soon as the desired stain is produced, which takes but a minute or two, the stain should be carefully drawn off with blotting paper and pure water run under the cover-glass. By this process all the details of division may be easily followed, as the chromatin stains very deeply, while the protoplasm remains almost colorless. Such preparations may be kept for some time in dilute glycerine but soon fade.

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*Strasburger—Hillhouse, Practical Botany—(p. 356).

†Campbell—" Staining of living nuclei," Arbeiten des Bot. Instituts zu Tübingen, 1888.

The isolated spore mother-cells are characterized by their thick, irregular walls, which remain intact until the final divisions are completed. The resting nucleus of the mother-cell is large, and has a very distinct membrane. It shows an indistinctly filamentous structure, and in *Allium* has a large nucleolus at one side which colors but little, and from its position is sometimes known as "para-nucleus." It is probable that the "segments" or chromatin filaments, which later become so distinct, are even in the resting nucleus entirely disconnected, and not confluent as was formerly supposed. In *Podophyllum* the nucleolus is much less conspicuous, and early becomes indistinguishable.

As the nucleus prepares for division it increases very much in size, and the chromatin filaments become much more distinct, appearing as a tangled coil of threads, nearly filling the cavity of the nucleus (Pl. CIII. Fig. 2). These threads do not color evenly, but consist of two substances, one of which does not color at all, and later is scarcely to be seen; the other (chromatin) staining very intensely, and in the earlier stages of division showing more or less distinctly as separate portions (microsomes). These later seem to coalesce more or less completely, so that the segments of the later division-stages stain uniformly and very intensely.

The next stage (Fig. 3) shows the filaments much shortened, and very evident. They color also much more uniformly and lie in the colorless nuclear cavity, which is still separated from the cell-plasm by an evident membrane. The latter soon disappears, however, leaving the short, thick segments free in the center of the cell (Figs. 4, 5). *Podophyllum* is especially favorable for showing this stage and those immediately following, on account of the small number (about ten) of the nuclear segments. These arrange themselves in the form of a disc (nuclear-plate) across the center of the cell (Figs. 4-7K.), and each segment splits longitudinally into two similar daughter-segments, which are usually more or less distinctly bent, often being V-shaped (Fig. 6). Sometimes this division of the segments seems to begin before the disappearance of the nuclear membrane (See Fig. 3).

When the nuclear-plate is complete there may be seen, though this is often difficult in acetic acid preparations, fine lines (Fig. 7F.) converging near the poles of the cell, so as to form a spindle-shaped figure with the nuclear-plate at the equator. The whole constitutes the "nuclear-spindle," and the fibers of which it is composed, the "spindle-fibers" (*Spindelfasern* of the German authors). The spindle-fibers probably correspond in number to the segments of the nuclear-plate, but this is difficult to prove. For studying this point, alcoholic material is preferable.

As soon as the nuclear-spindle is completed the daughter segments separate and travel along the spindle-fibers to the poles of the spindle, (Figs. 8, 9). When viewed from the poles they often show a very regular, stellate arrangement, the V-shaped segments being arranged in a circle with the free ends outward.

As the two sets of segments separate, fine lines may be detected connecting the young nuclei (Pl. CIII. Figs. 8-12 V.) These "connecting threads" (*Verbindungsfäden*) are much more numerous than the spindle-fibers. After reaching the poles, the daughter nuclei pass through much the same phases, but in reverse order, that preceded the division of the primary nucleus (see figs. 10-13). About the time that the nuclear membrane becomes evident, or sometimes a little earlier, a plate composed of small granules appears in the middle of the space occupied by the connecting threads, and careful examination shows them to be knot-like thickenings of the latter (Fig. 11 C.) This structure is the "cell plate," and usually is the beginning of a division wall (Pl. CII. Figs. 12-14). In this case (*Allium*) new connecting threads are formed, running to the circumference of the cell plate, thus increasing its size until finally it reaches completely across the cell (Fig. 13). The separate microsomes of which it is composed now coalesce and form a complete membrane, that divides the mother cell into two. In *Podophyllum* and most other dicotyledons, the primary cell-plate disappears without forming a continuous membrane, though the indication of a division is often evident even after the connecting threads are no longer evident. (Pl. CIII. Fig. 13).

Each of the daughter-nuclei now goes through the same process described for the primary nucleus, but when the ripe spores are arranged tetrahedrally, as in *Podophyllum*, the four nuclei resulting from the final division arrange themselves about the periphery of the cell at equal distances from each other, and connecting threads are formed between them in all directions (Pl. CIII. Fig. 17). A cell-plate is now formed between each pair of nuclei, extending to the center of the cell, thus forming four tetrahedral cells—the young pollen-spores. The division wall is formed in part also by a ridge which projects inward from the wall of the mother cell (Fig. 19). The division walls become finally very thick, so that the young pollen spores appear to be embedded in a thick colorless matrix. This thick wall is finally absorbed, setting free the spores and these soon acquire their characteristic covering.

In *Allium* and most monocotyledons, the spores are of the "bilateral" form, and in these a dividing membrane is formed after each nuclear division. The division of the daughter-nuclei in these frequently takes place in planes at right angles to each other (Pl. CII. Figs. 10, 14).

Direct nuclear divisions (*i. e.*, constriction of the nucleus without any further change) is known in a few cases, but always takes place in the older cells. The older parenchyma cell of the stem of *Tradescantia Virginica* and the internodal cells of *Chara* and

Nitella furnish common instances. They may be treated with acetic acid and gentian-violet as described, in the latter case cutting the long cells across and forcing out the contents with a needle or fine forceps.*

EXPLANATION OF FIGURES.

(Plate CII.)

Fig. 1.—Filament of *Nostoc* × 350.
2–6.—*Cladophora* (sp?) Showing process of cell-division followed in the same cell. Fig. 2, drawn at 9:30 A. M. Fig. 6, 2:05 P. M. × 300.
7 —A much larger cell of the same × 175.
8.—A dividing cell of *Spirogyra* (sp?) × 300.
9.—A Desmid in process of division ; n. the nucleus ; p. pyrenoid.
10–14.—Final divisions of the pollen-spores of *Allium Canadense*. Acetic acid, gentian violet × 350. In Fig. 10 the nuclear spindle in the left-hand cell is seen from the pole.

(Plate CIII.)

Division of the pollen-spores of *Podophyllum peltatum*. All the figures were drawn from acetic acid, gentian violet preparations, and all but six are magnified about 625 diameters, the latter about 1200.
Figs. 1–13.—Division stages of the primary nucleus of the mother-cell. Figs. 5–6 seen from the pole, the others from the side.
14–20.—Division of the secondary nuclei and formation of the spores.
21.—Two young isolated pollen-spores.
N-Nucleus; K-Nuclear-plate ; F-Spindle-fibers ; C-Cell-plate.

On the Naming of "Forms," in the New Jersey Catalogue.

In a recent number of the BULLETIN, (Vol. xvi. 272) when remarking on Mr. Cockerel's paper on the naming of slight varieties, I stated that I had introduced the term "forma" into the Catalogue of Plants found in New Jersey, as a rank to include physiological deviations or variations, such as color, odor and size, reserving for the term "varietas" such as are manifestly structural. I noted at that place that it was indeed difficult to rigidly separate even these characters, so that very slight structural deviations in the size of organs or their number or amount of division, might best come under the rank of "forma." I think that it is only in the latter sense that the term has been used by European authors, especially of the German school, and in their microscopic habits of thought, attempts have been made to attach

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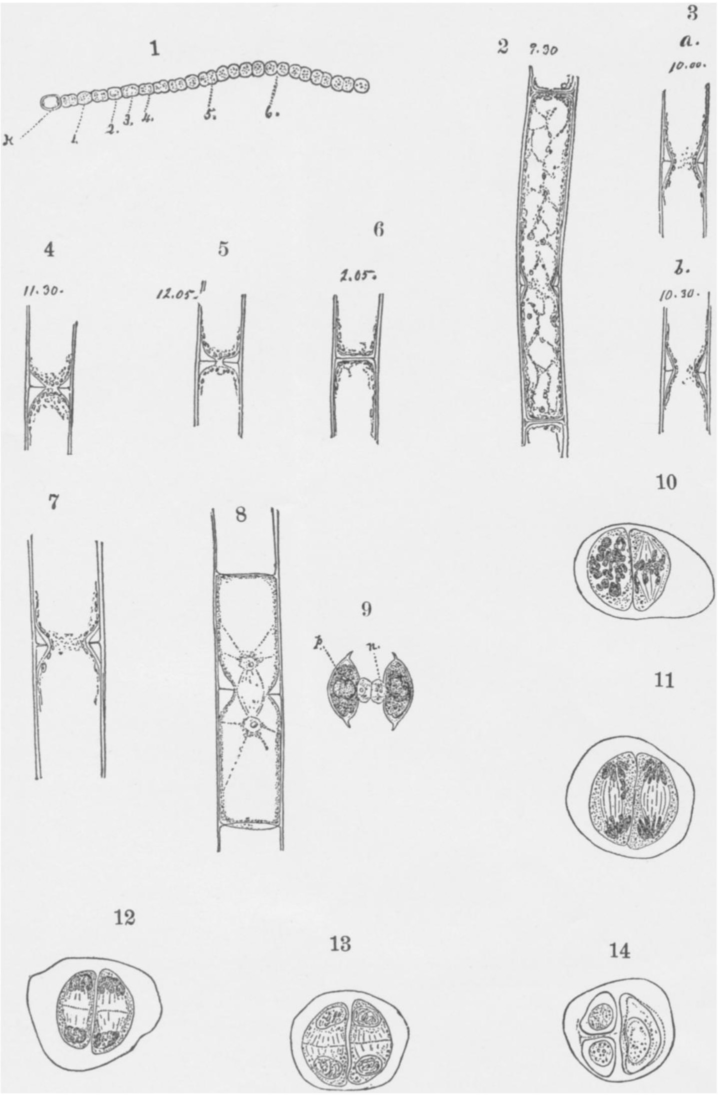
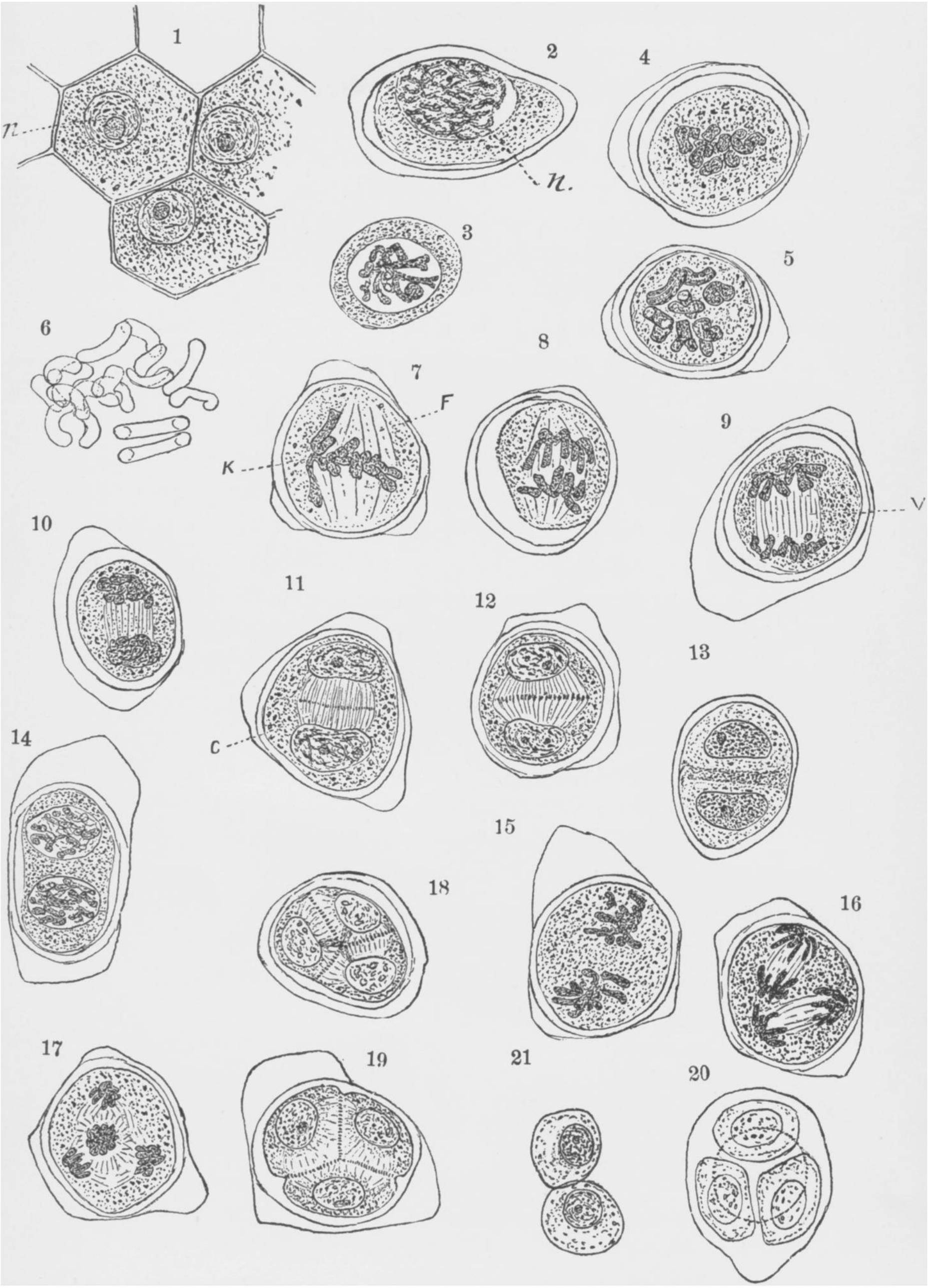
*See Strasburger-Hillhouse, p. 369 for *Tradescantia* ; "Botanisches Practicum," 1st edit. p. 516 for *Chara* and *Nitella*.

BULLETIN OF THE TORREY BOTANICAL CLUB. Plate CII.



STUDIES IN CELL-DIVISION. DOUGLAS H. CAMPBELL.

BULLETIN OF THE TORREY BOTANICAL CLUB. Plate CIII.



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